

Preliminary Examination of Non-Occlusal Dental Microwear in Anthropoids: Implications for the Study of Fossil Primates

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ABSTRACT Most studies of microscopic wear on non-human primate teeth have focused on the occlusal surfaces of molars. Recent analyses of the buccal surfaces of human cheek teeth have demonstrated an association between diet and dental microwear on these surfaces as well. In the current study, we examine microwear on both the buccal and lingual surfaces of non-human primate molars to assess the potential of these surfaces to reveal information concerning anthropoid feeding behaviors. We compare frequency of microwear occurrence in 12 extant and 11 fossil anthropoid species. Among the living primates, the occurrence of microwear on non-occlusal surfaces appears to relate to both diet and degree of terrestriality. The implications of this research for the inference of feeding behaviors and substrate use in fossil cercopithecoids are discussed. © 1996 Wiley-Liss, Inc.

For nearly two decades, microwear researchers have examined the occlusal surfaces of human and non-human primate molars for clues about the material properties of food items eaten (see Teaford [1994] and Ungar [1992a] for review). Studies of dental microwear of human populations have suggested that non-occlusal (buccal and lingual) surfaces can also provide important insights into subsistence patterns, particularly in agriculturalists and hunter-gatherers (Fine and Craig, 1981; Lalueza Fox and Pérez-Pérez, 1993; Lalueza et al., 1993; Puech, 1976, 1982). To date, however, there have been no studies of non-occlusal molar microwear in non-human primates. This paper reports on a preliminary examination of microscopic use-wear on the buccal and lingual surfaces of the molars of extant and extinct anthropoid primates. Our conclusion is that microwear incidences on these surfaces probably reflect feeding behaviors of extant anthropoids and may provide important

information about the diets of fossil primates.

HISTORICAL REVIEW

Dietary signals of dental microwear can be difficult to isolate or distinguish because a number of factors likely contribute to patterns observed on wear surfaces. For example, there has been considerable debate over the role of attrition (i.e., wear caused by contact between opposing tooth surfaces during chewing) in the formation of dental microwear features. Several early researchers attempted to identify microscopic traces of attrition (e.g., Butler, 1973; Dahlberg and Kinzey, 1963; Kay and Hiiemae, 1974; MacIntyre, 1966). Some subsequent investiga-

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tors argued that microwear can only be caused by abrasion, or tooth contact with external abrasives harder than dental enamel (Gordon, 1982, 1984; Rensberger, 1978; Teaford and Walker, 1983). Still, others have maintained that attrition can cause wear (Grine, 1981; Puech, 1984; Puech et al., 1981; Teaford and Runestad, 1992; Walker, 1984), although it may not be *abrasive* wear. For instance, differential enamel hardness (due to varying apatite c-axis directions) of opposing teeth may allow teeth to scratch one another during mastication, or microscopic contacts between enamel asperities may lead to high occlusal pressures and *adhesive* wear as enamel prisms are plucked from one of the opposing surfaces (Puech, 1984; Teaford and Runestad, 1992; Walker, 1984).

These debates have led some to examine non-occlusal surfaces for wear patterns that might provide clues regarding foods eaten. Since buccal and lingual molar surfaces do not regularly come into contact with those of opposing teeth, microwear on these surfaces should be free from the potentially confounding effects of attrition. In the late 1970s and early 1980s, Puech and coworkers (Puech, 1976, 1982; Puech and Pant, 1980; Puech et al., 1980) and Fine and Craig (1981) examined buccal surfaces of the cheek teeth of non-industrial peoples with differing subsistence patterns in attempts to distinguish microwear resulting from meat consumption from that caused by vegetable matter. Lalueza and coauthors (1993; Lalueza Fox and Pérez-Pérez 1993) have recently brought attention back to non-occlusal microwear studies by once again relating differences on the buccal faces of human molars to differences in subsistence practices. The study described here provides a first glimpse at non-occlusal microwear on non-human primate molars and its potential to reveal information about diet and tooth use.

MATERIALS AND METHODS

In this investigation, we examined microscopic wear on the buccal and lingual surfaces of the mandibular second molars (M_2 s) of individuals representing 12 extant an-

TABLE 1. Taxa examined during this study

Extant taxa	Fossil taxa
<i>Alouatta seniculus</i>	<i>Cercocebus</i> sp.
<i>Cebus apella</i>	<i>Cercopithecoides</i> sp.
<i>Cebus olivaceus</i>	<i>Colobus</i> sp.
<i>Cercocebus albigena</i>	<i>Papio</i> sp.
<i>Cercocebus torquatus</i>	<i>Paracolobus</i> spp.
<i>Colobus guereza</i>	<i>Parapapio</i> sp.
<i>Hylobates lar</i>	<i>Prohylobates</i> sp.
<i>Nasalis larvatus</i>	<i>Rhinocolobus</i> sp.
<i>Papio cynocephalus</i>	<i>Theropithecus darti</i>
<i>Papio ursinus</i>	<i>Theropithecus oswaldi</i>
<i>Procolobus badius</i>	<i>Victoriapithecus macinnesi</i>
<i>Theropithecus gelada</i>	

thropoid species and 11 fossil cercopithecoid taxa (Table 1).

Extant sample

Extant specimens examined for this study were all wild-caught adults ($n = 10$ to 21 per species) housed at the National Museum of Natural History in Washington, D.C., the Field Museum of Natural History in Chicago, and the collections at the University of California at Berkeley. Taxa were chosen to represent a wide range of trophic adaptations. While the diets of living primates can be extremely variable, and there is often little consistency in observational methods and sampling techniques among field primatology studies, it is clear that primates do exhibit identifiable food preferences and feeding adaptations. For example, among the taxa considered here, *Cercocebus* spp., *Hylobates lar*, and *Cebus* spp. are primarily frugivorous (e.g., Gittens and Raemakers, 1980; Freese and Oppenheimer, 1981; Terborgh, 1983; Waser, 1984; Robinson, 1986), although there is considerable variation in diet among these taxa (e.g., *Cercocebus albigena* and *Cebus apella* consume harder fruits more often than congeners examined here). In contrast, *Colobus guereza*, *Procolobus badius*, *Nasalis larvatus*, and *Alouatta seniculus* are all to some degree folivorous, although there are clearly differences in diet among these primates as well (e.g., Bennett and Davies, 1994; Bennett and Sebastian, 1988; Clutton-Brock, 1975; Gaulin and Gaulin, 1982; Kawabe and Mano, 1972; Kern, 1964; Morbeck, 1977; Oates, 1977, 1994; Rose, 1978; Struhsaker, 1978). For example, among colobines, while *Colobus guereza* de-

depends a great deal on leaves, *Procolobus bad-ius* and *Nasalis larvatus* more often consume unripe fruits, shoots, seeds, and other food items. Finally, baboons (*Papio* spp., *Theropithecus gelada*) often consume grass seeds, roots, and other grassland food items (e.g., Altmann and Altmann, 1970; Dunbar and Dunbar, 1975; Iwamoto, 1993; Jolly, 1970).

The taxa studied here can also be distinguished by other aspects of their feeding ecology. For example, primates often differ from one another in their feeding heights and substrate preferences. While baboons are predominantly terrestrial, *Cercocebus* spp. (especially *C. albigena*) are more arboreal (e.g., Jolly, 1970; Melnick and Pearl, 1986; Waser, 1984). *Cebus* spp. also apparently prefer feeding in the canopy, but they often descend to the ground to forage and eat (e.g., Robinson, 1986; Ungar, 1990). The colobines are generally more arboreal, although some, such as *Nasalis larvatus*, may descend to the ground to feed at least on occasion (e.g., Curtin, 1980; Kawabe and Mano, 1972; Oates and Davies, 1994). In contrast, *Hylobates lar* prefers the middle and upper canopy and rarely if ever descends to, let alone feeds on, the ground (e.g., Ungar 1992b).

Fossil sample

Examinations of the fossil taxa were conducted using high-resolution replicas of specimens from the Kenya National Museums. Casts were prepared following conventional procedures (Beynon, 1987; Rose, 1983; Teaford and Oyen, 1989) that have repeatedly been shown to reproduce faithfully features to a fraction of a micron, a resolution more than sufficient for microwear feature identification. Fossil taxa were represented by one to 12 individuals per taxon. These specimens included Plio-Pleistocene colobines and cercopithecines from the Turkana Basin, Laetoli, and Olduvai Gorge; as well as primitive cercopithecoids (i.e., *Victoriapithecus*, *Prohylobates*) from Maboko Island and the Turkana Basin. Due to excessive postmortem wear on the teeth of some specimens, sample sizes for many fossil taxa were drastically reduced. Further, it was necessary to consider some fossil colobine congeners as a single group to increase sample

sizes. Still, sample sizes were large enough ($n \geq 10$) for some species (i.e., *Theropithecus oswaldi*, *Victoriapithecus macinnesi*, and *Parapapio* spp.) to allow reasonable comparisons with the extant taxa.

Methods of analysis

Original specimens or high-resolution replicas of all individuals were examined at 60 \times using a transmitted light microscope. M_2 s were chosen because of their 1) central position in the molar tooth row, 2) location above the opening to the cheek pouch in cercopithecines (see below), 3) abundance in fossil primate assemblages, and 4) use in conventional occlusal surface microwear analyses. The presence or absence of microwear on the middle one-third of the buccal surface of the hypoconid and the lingual surface of the entoconid¹ of each specimen was recorded as observed (see Fig. 1). When microwear was present, the surface was usually covered by a great number of striations, and the difference in pattern between presence and absence was very clear. Many of the fossil replicas were also examined by scanning electron microscopy (SEM) to distinguish artifacts caused by taphonomic processes or specimen preparation from antemortem microwear (following Teaford [1988]). Resulting data matrices for the extant taxa were analyzed using the BIOM (Applied Biostatistics, Inc.) statistical package.

The occurrences or incidences of microwear were analyzed in two ways. First, a randomized blocks design was used to compare microwear incidences between surfaces (i.e., to determine whether buccal and lingual surfaces showed comparable incidences for a given taxon). Percentages of individual specimens that showed microwear on each surface were computed, and data were rank transformed. The transformed data were analyzed using a two-factor analysis of variance (ANOVA) without replication, with species and surfaces as the independent variables. This test is equivalent to Friedman's method for randomized blocks and is free of the distribution assumptions

¹The metaconids of three of the 53 fossil specimens were examined because of poor preservation of entoconid surfaces.

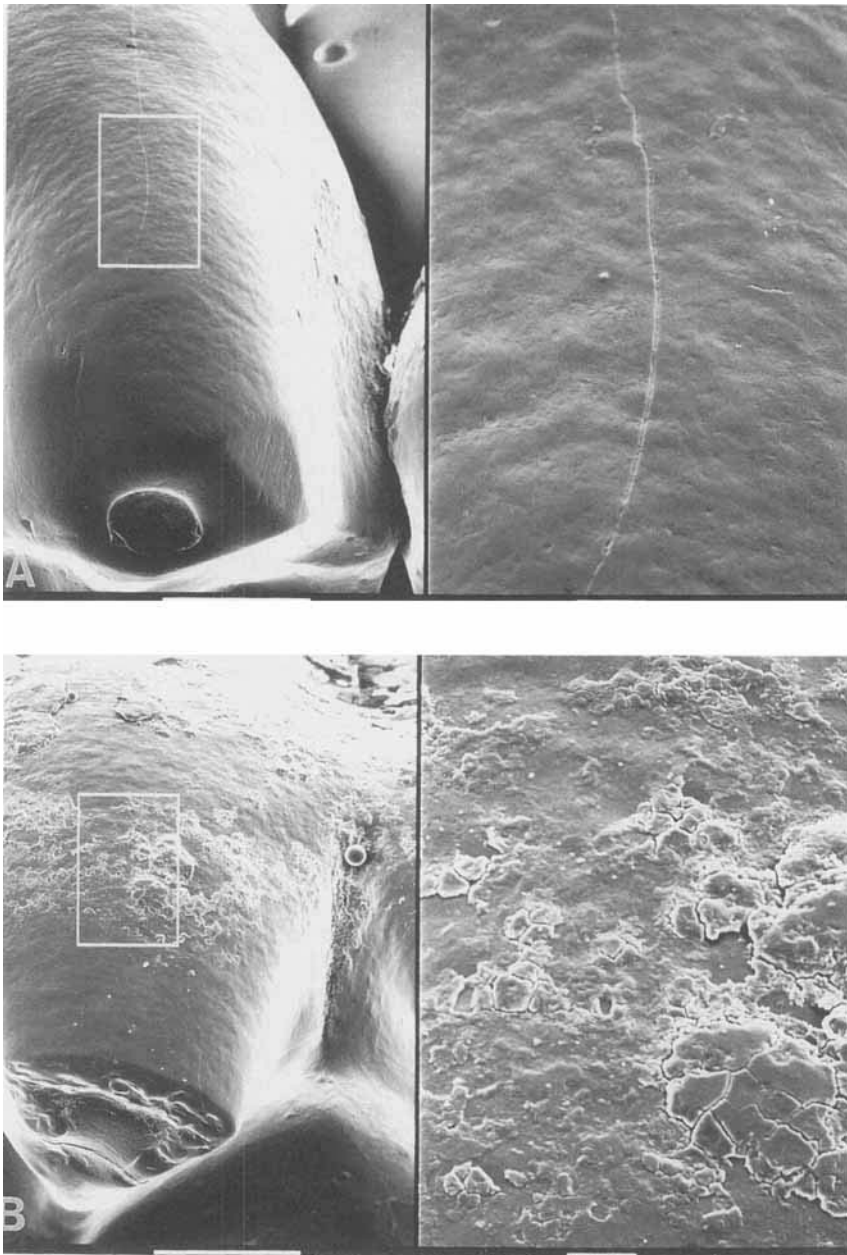
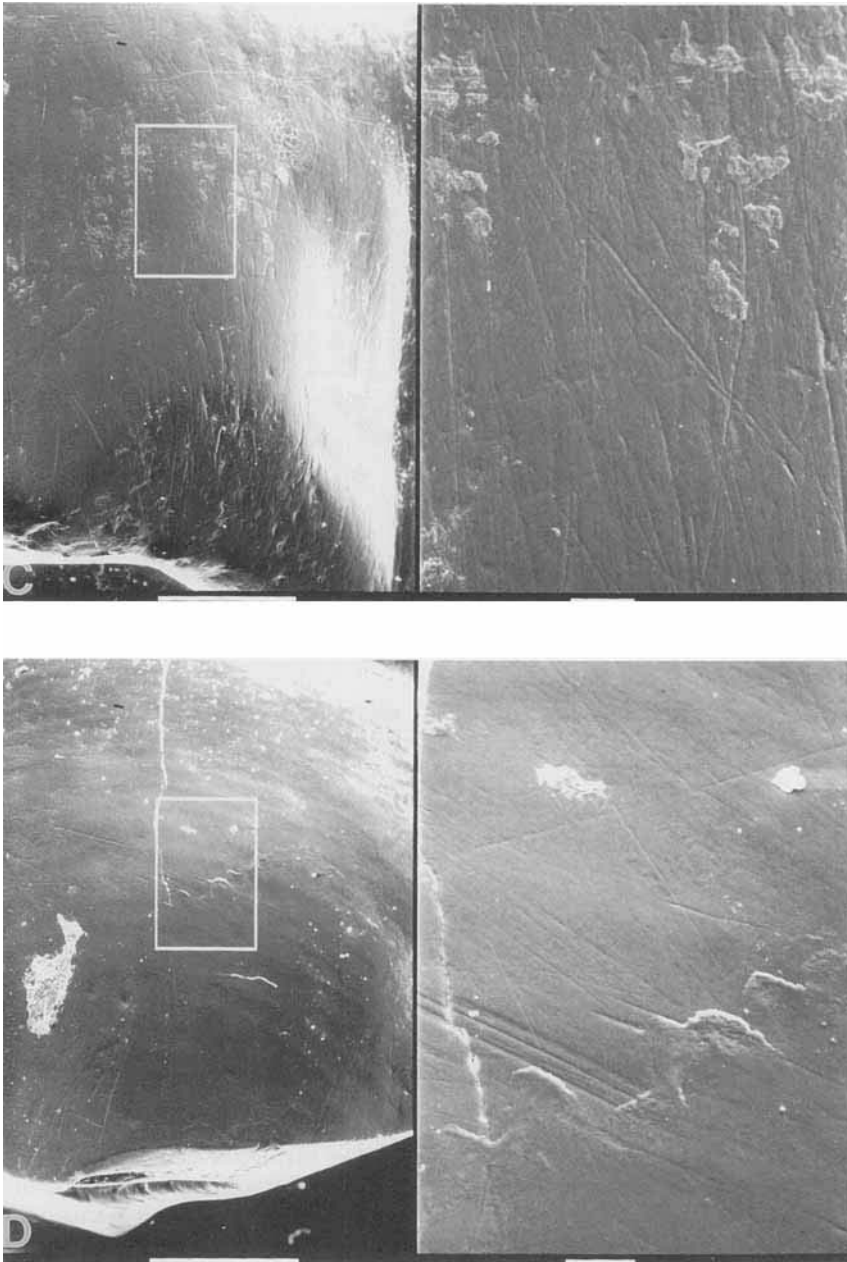


Fig. 1. The areas sampled in this study. The cusp examined and area sampled are presented on the left and right, respectively, for each photomicrograph. Scale bars on the left and right of each photomicrograph indicate 1 mm and 100 μ m, respectively. Surfaces presented are as follows: **A**) *Colobus guereza* (NMNH 452620) buccal surface of the hypoconid of LM_2 ; **B**) *Colobus guereza*

(NMNH 452620) lingual surface of the entoconid of LM_2 ; **C**) *Papio cynocephalus* (OM 7241) buccal surface of the hypoconid of LM_2 ; **D**) *Papio cynocephalus* (OM 7402) lingual surface of the entoconid of LM_2 . Note the presence of microwear striations on buccal and lingual surfaces of *Papio cynocephalus* but not *Colobus guereza*.



inherent in parametric tests (Conover and Iman, 1981).

Second, differences in the incidence of microwear between pairs of extant taxa were also assessed using two-way contingency tables. Because of the presence of empty cells, Fisher's exact tests were used to compare

each pair of species for buccal and lingual surface microwear presence (Zar, 1984). A very conservative experiment-wise error rate ($\alpha' = .001$ where $\alpha' = \alpha/K$, $\alpha = .05$ and $K = 43$) had to be employed because of the great number of pair-wise tests necessary to allow comparison of all pairs of taxa for

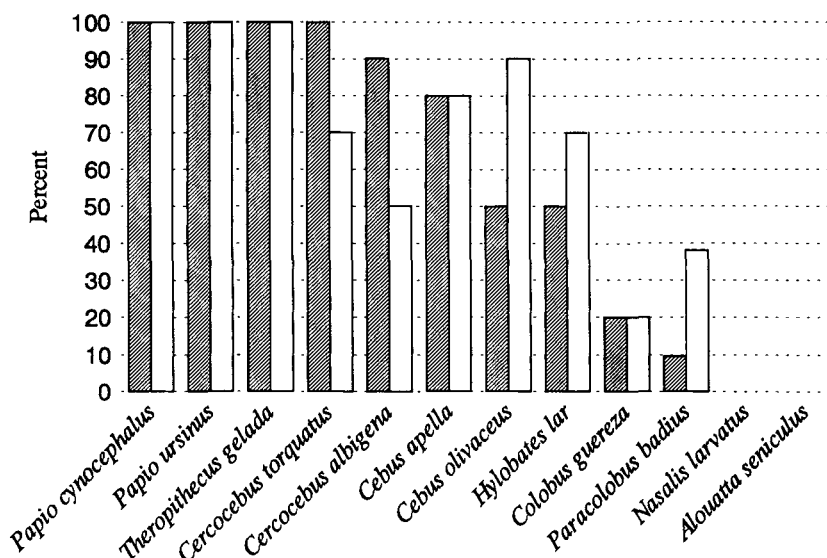


Fig. 2. Microwear incidences for the extant sample. The chart shows percentage of specimens for each species with microwear on their buccal (hatched bars), and lingual (open bars) surfaces.

presence/absence of microwear on both the buccal and lingual surfaces.

RESULTS

Results indicate that many of the extant primate taxa studied differ from one another in whether they have microwear on non-occlusal surfaces of their M_2 s (Figs. 1, 2; Table 2). Results are similar whether considering buccal or lingual faces (Figs. 1, 2; Tables 3, 4). The cercopithecines (*Papio* spp., *Theropithecus gelada*, *Cercocebus* spp.) show microwear on these surfaces more often than do the colobines (*Colobus guereza*, *Procolobus badius*, *Nasalis larvatus*) and *Alouatta seniculus*. The capuchins (particularly *Cebus apella*) also display microwear on more of their buccal and lingual surfaces than do the colobines and *Alouatta seniculus*. Further, *Hylobates lar* exhibits intermediate incidences of non-occlusal surface microwear.

As for the fossil taxa, *Theropithecus oswaldi*, *Victoriapithecus macinnesi*, and *Parapapio* sp. show antemortem microwear on most or all surfaces examined. These taxa fall neatly within the extant cercopithecine range (Table 2). Further, less well-represented fossil cercopithecines also appear to show patterns that would set them within

this group (although sample sizes are so small as to make such comparisons tentative). Interestingly, of the fossil colobines examined, some (*Paracolobus* spp. and *Colobus* sp.) are most similar to their modern counterparts, whereas others (*Rhinocolobus* sp. and *Cercopithecoides* sp.) are more similar to modern cercopithecines in microwear incidence (Table 2).

DISCUSSION

Extant taxa

The pattern of differences observed for the extant taxa strongly suggests that variation in the incidence of non-occlusal microwear reflects differences in feeding adaptations. There are two key elements to microwear formation on non-occlusal surfaces. First, these surfaces must regularly come into contact with food items. One might expect that larger foods (e.g., large, tough fruits) would more often extend down the sides of the teeth and into the vestibule than would smaller or more planar foods (e.g., leaves). Second, those food items eaten must contain abrasives capable of scratching tooth enamel.

Most microwear researchers acknowledge two potential sources of such abrasives: sili-

TABLE 2. Microwear incidence data¹

Taxon	n	Buccal		Lingual	
		+	-	+	-
I. Taxa with n ≥ 10					
<i>Theropithecus gelada</i>	13	13	0	13	0
<i>Theropithecus oswaldi</i> ²	10	10	0	10	0
<i>Papio cynocephalus</i>	10	10	0	10	0
<i>Papio ursinus</i>	10	10	0	10	0
<i>Victoriapithecus macinnesi</i> ²	12	12	0	12	0
<i>Cercocebus torquatus</i>	10	10	0	7	3
<i>Parapapio</i> spp. ²	11	11	0	10	1
<i>Cercocebus albigena</i>	10	9	1	5	5
<i>Cebus apella</i>	10	8	2	8	2
<i>Cebus olivaceus</i>	10	5	5	9	1
<i>Hylobates lar</i>	10	5	5	7	3
<i>Colobus guereza</i>	15	3	12	3	12
<i>Paracolobus badius</i>	21	2	19	8	13
<i>Nasalis larvatus</i>	10	0	10	0	10
<i>Alouatta seniculus</i>	10	0	10	0	10
II. Fossil taxa with n < 10					
<i>Papio</i> sp ²	7	7	0	7	0
<i>Cercocebus</i> sp. ²	4	4	0	4	0
<i>Prohylobates</i> sp. ²	1	1	0	1	0
<i>Theropithecus darti</i> ²	1	1	0	1	0
<i>Cercopithecoides</i> sp. ²	3	3	0	1	2
<i>Paracolobus</i> spp. ²	3	1	2	1	2
<i>Rhinocolobus</i> sp. ²	2	2	0	2	0
<i>Colobus</i> sp. ²	1	0	1	0	1

¹ This table shows the No. of specimens from each species with (+) or lacking (-) microwear on the buccal and lingual surfaces examined.

² Fossil taxon.

ceous phytoliths or particles in or on plant structures (e.g., Baker et al., 1959; Kay and Covert, 1983; Lucas and Teaford, 1995; Ungar, 1994) and exogenous grit from soil or dust (e.g., Healey and Ludwig, 1965; Puech, 1986; Ungar, 1994; Ungar et al., 1995; Walker, 1976; Walker et al., 1978). One might expect that primates that habitually eat foods rich in phytoliths or those that habitually feed on or near the ground would more often show microwear on their tooth surfaces than those that do not. Because fruits are not more likely to contain phytoliths than are leaves (Piperno, 1989), lower incidences of microwear among the more folivorous primates are more liable to reflect differences in the amount of grit on foods eaten. Although potentially abrasive dust can be found on food items taken in the canopy to some extent (Ungar et al., 1995), much more abrasive grit is likely introduced from the ground during terrestrial feeding bouts (Pastor, 1993; Ungar, 1990, 1992b; Walker, 1976). Thus, perhaps differences in microwear incidence relate, in part, to differences in the incidences of terrestrial feeding events.

These expectations are more or less borne out by the data for the extant primates. The more terrestrial and/or frugivorous cercopithecines (i.e., *Theropithecus gelada*, *Papio* spp., and *Cercocebus* spp.) show high incidences of microwear on both buccal and lingual surfaces, whereas the more arboreal and folivorous colobines (i.e., *Colobus guereza*, *Procolobus badius*, *Nasalis larvatus*) show lower incidences. New World monkeys also show this apparent association between degree of terrestriality/frugivory and the presence of non-occlusal microwear. The more terrestrial and frugivorous *Cebus* spp. more often show microwear than does the more arboreal and folivorous *Alouatta seniculus* (see also Ungar 1990). Interestingly, the highly arboreal yet frugivorous *Hylobates lar* is intermediate in microwear feature occurrence. An assessment of the relative effects of feeding substrate and food preferences on microwear incidences will require further investigation, but it is apparent that these causal factors are both likely to contribute to microwear differences among the taxa. A case in point is provided by *Theropithecus gelada*, which is terrestrial

TABLE 3. Paired comparisons tests¹

	SS	df	MS	F	p
I. RT-1					
Species	1027.000	11	93.364	11.994	.0001
Surface	0.375	1	0.375	0.048	.8306
Remainder	85.625	11	7.784		
II. RT-2					
Species	256.000	11	23.275	12.190	.0001
Surface	0.000	1	0.000	0.000	1.0000
Remainder	21.000	11	1.909		

¹ Comparisons of rank-transformed percentage incidence of microwear occurrence between the buccal and lingual surfaces. Results are given for both Conover and Iman's (1981) RT-1 and RT-2 methods of data ranking.

and yet feeds primarily on planar grass leaves. Unlike the colobines, *T. gelada* shows a great deal of non-occlusal microwear. Could this be caused by long strands of grass rubbing on the sides of the tooth? Could it be caused by the retrieval of abrasive food from cheek pouches? If so, why would it also have scratches on its lingual surfaces? Only further work will tell.

The presence of non-occlusal microwear on the molars of *Cebus* and *Hylobates* indicates that there is not a strict correspondence between the presence of non-occlusal microwear and the presence of cheek pouches. Likewise, the presence of scratches on the lingual surfaces of cercopithecine lower molars suggests that the presence of non-occlusal microwear is probably tied to the diet of the animal in question rather than the presence of cheek pouches per se.

Fossil taxa

These results hold interesting implications for the interpretation of fossil cercopithecoid diets. First, in terms of *non-occlusal* microwear, the reconstructed diets of the fossil cercopithecines are generally similar to those of their modern counterparts, whereas some fossil colobines (*Paracolobus* and *Colobus*) are inferred to have had similar diets to their modern counterparts and others (*Cercopithecoides* and *Rhinocolobus*) are not. Differences among the colobines may relate, in part, to differences in the degree of terrestriality of some of the extinct species (e.g., *Cercopithecoides* probably spent a considerable amount of time on the ground) (Birchette, 1981; Leakey, 1982). However, this does not explain the similar

pattern observed in the more arboreal *Rhinocolobus* (Leakey, 1982).

Interestingly, the molar occlusal microwear of the fossil monkeys paints a different picture. The fossil cercopithecines are the ones whose diets are reconstructed to be different from those of their modern counterparts, showing similar amounts of microwear but far less pitting than expected (Lucas and Teaford, 1994; Teaford and Leakey, 1992). By contrast, fossil colobines look similar to their modern counterparts.

Why do the results of the occlusal and non-occlusal microwear studies lead to these apparently different interpretations? As it turns out, these differences may actually help us better understand fossil monkey feeding behavior. The similarities between extant and fossil monkeys in the amount of occlusal microwear suggest that the amount of abrasives in their diets was similar. The only possible exception lies in *Cercopithecoides*, where there is a hint of more microwear, but small samples make interpretations difficult (Teaford and Leakey, 1992). As large occlusal enamel pits have been repeatedly tied to the presence of hard objects in the diet (Harmon and Rose, 1988; Teaford, 1994; Teaford and Walker, 1984), the difference in enamel pitting between modern and fossil cercopithecines probably reflects a lack of hard objects in the diets of the fossil forms. With this in mind, the similarities in *non-occlusal* microwear between modern and fossil cercopithecines probably reinforce the idea that these monkeys had similar amounts of abrasives in their diets. It also suggests that the size and shape of modern and Plio-Pleistocene cercopithecine food might have been similar (e.g., including large siliceous or grit-covered fruits, roots, or seeds). The more variable patterns of non-occlusal microwear in the fossil colobines may be yet another indication that the Plio-Pleistocene colobines had a more variable diet and/or substrate preference than do their modern counterparts (Benefit, 1987; Birchette, 1982; Leakey, 1982).

Another point to be noted from this study is the similarity between the victoriapithecines and the cercopithecines in non-occlusal microwear. As in studies of the dental morphology (Benefit, 1987, 1995), and occlusal

TABLE 4. Fisher exact test probabilities*

	<i>P. ursinus</i>	<i>T. gelada</i>	<i>C. torquatus</i>	<i>C. albigena</i>	<i>C. apella</i>	<i>C. olivaceus</i>	<i>H. lar</i>	<i>C. guereza</i>	<i>P. badius</i>	<i>N. larvatus</i>	<i>A. seniculus</i>
I. Buccal surface											
<i>P. cynocephalus</i>	1	1	1	.500	.474	.016	.000	.000	.000	.000	.000
<i>P. ursinus</i>		1	1	.500	.474	.016	.016	.000	.000	.000	.000
<i>T. gelada</i>			1	.435	.178	.008	.008	.000	.000	.000	.000
<i>C. torquatus</i>				.500	.474	.016	.016	.000	.000	.000	.000
<i>C. albigena</i>					1	.141	.141	.001	.000	.000	.000
<i>C. apella</i>						.350	.350	.005	.000	.001	.001
<i>C. olivaceus</i>							1	.194	.022	.033	.033
<i>H. lar</i>								.194	.022	.033	.033
<i>C. guereza</i>									.630	.250	.250
<i>P. badius</i>										.548	.548
<i>N. larvatus</i>											1
II. Lingual surface											
<i>P. cynocephalus</i>	1	1	.2105	.016	.474	.500	.211	.000	.001	.000	.000
<i>P. ursinus</i>		1	.2105	.016	.474	.500	.211	.000	.001	.000	.000
<i>T. gelada</i>			.0678	.008	.178	.435	.068	.000	.000	.000	.000
<i>C. torquatus</i>				.410	.652	.334	1	.135	.135	.002	.002
<i>C. albigena</i>					.350	.141	.410	.194	.701	.033	.033
<i>C. apella</i>						1	.652	.005	.054	.001	.001
<i>C. olivaceus</i>							.334	.001	.009	.000	.000
<i>H. lar</i>								.034	.135	.002	.002
<i>C. guereza</i>									.295	.250	.250
<i>P. badius</i>										.032	.032
<i>N. larvatus</i>											1

* An experimentwise error rate $\alpha' = .001$ ($\alpha = .05$, $K = 43$ individual tests, $\alpha' = \alpha/K$) should be employed to assess significance.

microwear of *Victoriapithecus* (Lucas and Teaford, 1994; Teaford and Leakey, 1992), this would seem to lend further support to the idea that the last common ancestor of cercopithecoids included significant amounts of fruit, tubers, or perhaps even seeds in its diet (Benefit, 1987; Happel, 1988; Kay, 1977; Lucas and Teaford, 1994; Temerin and Cant, 1983).

Non-occlusal surface microwear and postmortem damage

Results presented here also bring up an important methodological issue. Dental microwear researchers who study fossils, or human remains from archaeological contexts, often must distinguish between "real" use-wear (i.e., that caused during an animal's lifetime) and postmortem wear. Up until now, the standard procedure has been to look for wear patterns on the tooth surface not normally subjected to wear during use (Grine, 1986; Teaford, 1988). If microwear is present on such surfaces, the specimen has frequently been excluded from further microwear analysis. The present study demonstrates that many extant primates show antemortem microwear on buccal and lingual molar surfaces. As a result, researchers should be more careful in using non-occlusal surfaces to assess taphonomic effects on dental enamel.

The best place to make such assessments is still on the interstitial facets which are formed by tooth-on-tooth contacts (Teaford, 1988). These facets are not exposed to abrasive foods in the same manner as the buccal or lingual surfaces of the tooth, and they are characterized by the presence of innumerable, prism-sized pits probably caused by enamel prism-plucking (Puech, 1984; Teaford and Runestad, 1992; Walker, 1984). Thus, if the interstitial facets show small pits, and the areas immediately adjacent to those facets do not, the tooth can probably be used in microwear analysis.

If for some reason the interstitial facets are not available for a specimen, microwear on the buccal or lingual surface of the tooth (i.e., off the wear facets) may also be useful, because it will rarely show microscopic pits in normal use, and the microwear will generally show a marked difference (in orienta-

tion, incidence, etc.) from the occlusal surface. If the buccal or lingual surfaces show pits, or an identical microwear pattern to that found on the occlusal surface, then the tooth probably cannot be used in microwear analysis. Obviously, given the complexities of taphonomic processes, researchers should also be aware of unusual wear patterns on any tooth surface, as some portions of the tooth may be subjected to significant postmortem wear while other portions may not.

SUMMARY AND CONCLUSIONS

In sum, results presented here strongly suggest that an examination of dental microwear on the buccal and lingual surfaces of non-human primate molars may reveal important information about diet and/or feeding substrate. The limits and potentials of this approach will require a great deal more work to evaluate. More conventional SEM microwear investigations will likely provide important insights in this regard. Quantitative studies of individual wear features may allow us to distinguish effects of diet from those of substrate use (see Ungar, 1994), improve the resolution with which we can reconstruct fossil primate diets, and perhaps even allow us to take another look at the cheek pouch question. Further analyses of buccal and lingual surfaces will also facilitate comparison of non-occlusal and occlusal surface microwear results. This may provide a more complete picture of microwear formation for the fossils, and thus improve our reconstructions based on occlusal surface studies.

The current investigation suggests the potential of this approach, especially given that a measure as coarse as presence versus absence of microwear alone can distinguish among extant taxa. It is particularly intriguing that some fossil primates show patterns comparable to those of closely related living species whereas others do not, and that extinct forms appear to differ from one another in microwear incidence on buccal and lingual M_2 surfaces. This implies that while the formation of non-occlusal surface molar microwear is bound to be a complicated process, it is still likely to have im-

portant implications for the inference of feeding adaptations in fossil primates.

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